Abundance, species richness, host utilization and host specificity of insect folivores from a woodland site, with particular reference to host architecture

by

Yves BASSET* and Daniel BURCKHARDT**

With 3 figures

ABSTRACT

We studied the local abundance, species richness, host utilization and host specificity of insect folivores associated with 10 deciduous woody and 10 perennial herbaceous plant species growing in a woodland site in the Swiss Jura. Regional species richness of insect folivores on their hosts, inferred from compilation of insect faunas for Central Europe, was highly correlated with local species richness, as estimated by a 7-month field survey. Woody hosts sustained more insect species and a higher proportion of chewers, than herbaceous plants which, in turn, sustained a higher proportion of leaf miners. Overall insect abundance was not affected by plant architecture. On average, 56 % of the species feeding upon a particular host were specialists, with no apparent effect of plant architecture, but proportions for herbaceous plants fluctuated from 0 to 100 %. At the regional scale, 85 % of the variance in herbivore species richness was explained by the height of the host, its taxonomic relatedness and its leaf water content. At the local scale, 88 % of the variance could be explained, with a significant contribution of host phenology. The variances explained by models describing other local variables - such as herbivore abundance, number of specialist species, proportions of ectophagous/endophagous species and leaf palatability - were generally lower, with, sometimes, a significant contribution of sampling effort. Although confirmation will be needed from more extensive studies, particularly encompassing plants growing in other habitats, we suggest that the influence of variables such as leaf water and host phenology may have been underestimated as predictors of herbivore species richness.

* 3 Ch. Chesnaie, 1219 Châtelaine, Switzerland; present address: Bishop Museum, 1525 Bernice Street, PO Box 19000A, Honolulu, Hawaii 96817 0916, USA.
** Département d'Entomologie, Muséum d'Histoire Naturelle, 1211 Genève 6, Switzerland.

INTRODUCTION

Since the seminal paper of SOUTHWOOD (1961) about the number of insect species associated with various British trees, there has been growing interest in the host-related determinants of insect species richness on particular plant species. These determinants include the abundance of the host and its distribution; its age of establishment; the number of habitats within which it grows; its taxonomic relatedness and isolation; its architecture and biomass; its leaf size and shape; and whether it is deciduous or evergreen (SOUTHWOOD, 1961; LAWTON and SCHRÖDER, 1977; LAWTON and PRICE, 1979; STRONG and LEVIN, 1979; BIRKS, 1980; CLARIDGE and WILSON, 1981, 1982; NEUVONEN and NIEMELÄ, 1981; RIGBY and LAWTON, 1981; FOWLER and LAWTON, 1982; KARBAN and RICKLEFS, 1984; KENNEDY and SOUTHWOOD, 1984; CORNELL, 1985; LEATHER, 1986; CORNELL and KAHN, 1989; JONES and LAWTON, 1991).

Most authors examined the whole herbivore community associated with particular plants, but some studies concerned restricted herbivore groups and/or restricted host taxa (above references). However, few studies attempted to predict the guild structure of herbivore communities (as represented by the number of species of chewers, sap-suckers, leaf miners and gall formers) from host-related variables, with the notable exception of CORNELL and KAHN (1989) analyzing data for British trees (KENNEDY and SOUTHWOOD, 1984). Among other things, these authors concluded that models centered on the specialist/generalist dichotomy may prove to be more satisfactory in explaining the organization of herbivore communities than models derived from the relative importance of guild categories. CORNELL (1989) also advised paying attention to the ratio between ectophages (i.e., chewers) and endophages (i.e., other guilds) on plant species. To date, there is no published attempt to examine the number of specialist species, or their relative proportion, within a particular plant community.

Usually, information about herbivore loads on particular host plants is compiled from published insect faunas. This practice provides reliable material for insect species richness analyses (e.g., NIEMELÄ and NEUVONEN, 1983; LEATHER, 1990) but presents several impediments to estimating the proportion of specialist and generalist species feeding on a particular plant using the entomocentric information provided by such literature. First, hosts for polyphagous species may not be extensively listed, hosts may be identified by their generic names only or by general quotations (such as "on herbaceous plants" or "on various trees and shrubs", etc.), and the quality of information is generally poorer for herbaceous plants than for trees (LEATHER, 1986). Second, in these faunas the apparent sampling effort (which is confounded with plant citation) is not identical among hosts: often sampling/mention of hosts of economic importance and/or of extended distribution is prevalent (see NIEMELÄ and NEUVONEN, 1983). Some correction for the sampling intensity is needed (e.g., KARBAN and RICKLEFS, 1983) but this is less important if species-area effects are to be demonstrated (REY *et al.*, 1981). However, sampling effort may be crucial when investigating the relative proportion of specialist species, because increasing sampling effort is likely to append a high number of generalist species to a particular host (i.e., if sampling is unlimited, all highly-generalist species present locally may eventually be collected on a certain plant).

Most studies of host-related deteminants in herbivore species richness used multiple regression for statistical analysis. Three points are worth noting regarding the models generated by such analyses. First, certain attributes of foliage, which may influence herbivores feeding on leaves, may not explain much of the variance of insects associated with the wood, reproductive organs and roots of the host. Care must be taken to exclude those from the analyses if particular attention is given to the predictive value of

TABLE 1.

Host plants investigated and the number of associated species of insect folivores recorded from the literature and collected during the survey. For aggregates, the first named species indicates the most common host.

Hosts	Plant family	Nospecto	Nospecie
a) Woody hosts			
Salix caprea L. and hybrids	Salicaceae	446	46
Corylus avellana L.	Betulaceae	186	31
Fagus silvatica L.	Fagaceae	122	38
Quercus petraea Lieblein -			
Q. robur L. - *Q. pubescens* Willd. aggr.	Fagaceae	445	48
Crataegus oxyacantha L. -			
C. monogyna Jacq. aggr.	Rosaceae	180	35
Sorbus aria Crantz and hybrids	Rosaceae	100	31
Acer opalus Miller and hybrids	Aceraceae	83	31
Fraxinus excelsior L.	Oleaceae	80	25
Lonicera xylosteum L.	Caprifoliaceae	88	20
Viburnum lantana L.	Caprifoliaceae	35	18
b) Herbaceous hosts			
Arum maculatum L.	Araceae	4	3
Paris quadrifolia L.	Liliaceae	5	3
Dentaria heptaphylla Villars	Cruciferae	27	13
Lathyrus vernus Bernh.	Leguminosae	53	8
Euphorbia amygdaloides L.	Euphorbiaceae	41	5
Mercurialis perennis L.	Euphorbiaceae	7	6
Orthilia secunda L.	Pyrolaceae	5	3
Melittis melisophyllum L.	Labiatae	8	8
Galium odoratum (L.) Scop.	Rubiaceae	17	5
Solidago virgaurea L.	Compositae	45	7

and imagines of aleyrodids were counted only. Sample time and number of sampling occasions were identical for each host. However, the foliar area sampled varied among hosts: one sampling occasion consisted of > 20 samples (one different plant each) for herbaceous hosts and 10 samples (one different branch or branchlet of 30 - 50 leaves) for woody hosts. In each sample, the number of young and mature leaves/leaflets were counted. For each host and sampling occasion the mean leaf area (measurements of five leaves, totals of lower and upper sides) was determined with a transparent grid. This enabled an estimation of the leaf area sampled in each sample. Herbivore abundances were corrected by total leaf area sampled and expressed as number of individuals per 500 cm^2 of leaf area (i.e., the sample size closest to the average sample size for all hosts). This allowed us to compare herbivore abundance between host plants and to compute an index of herbivore abundance averaged from all sampling occasions (variable Index, see below).

EVALUATION OF INSECT HOST-SPECIFICITY

Insect host-specificity was derived from the relevant literature (see next section) and, in cases of difficult identification, deduced from field observations. In addition, chewers

were tested for feeding on the 20 hosts. Two or more individuals, kept within glass vials with 100 % R.H., were presented with fresh leaves (young or mature) of study hosts for 24 h. Feeding was scored as follows: 0 (no feeding), 1 (attempting to feed), 10 (small consumption of foliage) and 100 (extensive consumption of foliage). A logarithmic scale was chosen to emphasize regular and extensive feeding. Prior to testing, insects were fed with leaves from their presumed host and allowed to reach late instars in order to avoid inclusion in the analyses of "incidentals" (insects which rest on the foliage and do not feed; variable Incid, see below), and poor correspondence between oviposition and performance which may occur in some instances (e.g., THOMPSON, 1988). Because host-specificity indicated by these feeding tests refers to laboratory conditions, it was preferred, when available, to use the information found in the literature, which is usually relevant to field conditions. Because of problems with identification of aphids, the species of this group could not be assigned to either specialists or generalists according to the literature. Since most aphids are specialists (BÖRNER, 1952), all species collected were assigned to this category.

VARIABLES RETAINED FOR STATISTICAL ANALYSES

We inferred the regional species richness of herbivores from the literature and the local species richness from our field sampling. The data were analyzed with forward step-wise multiple regression analyses. The following dependent variables were considered. First, an estimate of the number of insect folivores associated with the 20 hosts at the regional scale was obtained by scanning the following insect faunas from Central Europe (in a few cases Northern Europe) and their host plant records (variable Nospecto): Heteroptera (STICHEL, 1955-1962); Auchenorryhncha (OSSIANNILSSON, 1978-1983); Sternorrhyncha (BÖRNER, 1952; VONDRAČEK, 1957; ZAHRADNIK, 1963; KOSZTARAB and KOZAR, 1988); Coleoptera (FREUDE *et al.*, 1966-1983); Symphyta (Lorenz and Kraus, 1957); "Microlepidoptera" (SWATSCHEK, 1958; HANNEMANN, 1977; PALM, 1989; HERING, 1932); "Macrolepidoptera" (BECK, 1960; FORSTER and WOHLFAHRT, 1955, 1960, 1981); leaf miners (HERING, 1957); and gall formers (BUHR, 1964-1965). This literature also provided estimates of the regional richness in chewers, sap-suckers, leaf miners and gall formers for each plant species (variables Chwto, Sapto, Mineto, Gallto). Since we did not identify thrips, they were disregarded to ensure valid comparisons between regional and local scales. When generic host-records were available only, they were assumed to apply to the plant species considered.

An estimate of the local species richness of all insect folivores (and of particular insect guilds) within the study site was provided by the number of species recorded on each host during all sampling occasions (variables Nospecie (Table1), Chw, Sap, Mines and Galls). Other dependent variables included Index and Incid, already defined, the local number of specialist species (Speciali), the local percentage-ratio of specialist species (Ratiospe, %), of ectophagous and endophagous species (Ratioect and Ratioend, %), and the mean scores for each host in feeding experiments for young leaves, mature leaves and all leaves combined (Scoyoung, Scomatu and Scotot, units = relative scores). Since feeding tests involving insects and plants from which they were collected were excluded from the analysis, these scores represented a measure of plant palatability relatively independent of the number of chewers collected from the host.

The independent variables used in the analyses are defined in Table 2, and some only, due to space limitations, are detailed further in Appendix 1. Water content and specific weight of young and mature leaves were determined by oven-drying at 100 °C [20

discs punched from each host, collected on the same day, at noon, in late May (young leaves) and early August (mature leaves)]. Despite the difficulty of characterising host biochemistry, we attempted to use two different variables related to host chemical defenses. First, an index of the diversification of plant chemical defences was provided by the variable Chemic, which represented the number of broad categories of chemical compounds present in the host and known to be active against herbivores. The choice of the chemical categories followed ROSENTHAL and JANZEN (1979) and included: toxic non-protein amino-acids, cyanogenic compounds, alkaloids, glucosinolates, terpenoids, saponins, flavonoid pigments, tannins, other phenols, coumarins, cardenolides, phyto-ecdysones and accumulation of silica. This information was abstracted from HEGNAUER (1962-1989), GIBBS (1974) and RAFFAUF (1970). Second, an estimation of the isolation of host chemical defences was provided by the variable Disschem, which was the similarity measure (euclidean distance) with an average and hypothetical host possessing the most common categories of chemical defences (i.e., the categories found in more than 10 of the 20 study plants). In July 1990, the abundance of the 20 host-species was recorded in 50 plots of 10 x 10 m within the study site. These plots were representative of locations sampled and provided estimations of the local abundance of hosts (Locabund), their local distribution (Locadist) and aggregation (Aggrega). The variable Compac represented a measure of the compactness of host foliage. For herbaceous hosts, this was defined as the leaf area of the whole plant and for woody hosts as the total leaf area supported by 50 cm of branch.

Both dependent and independent variables were log (x+1) transformed (natural base) in order to satisfy the assumption of normality. In most cases, transformation of data improved the fit to the models. The step-wise multiple regressions were computed with α-to-enter/remove = 0.150 (BENDEL and ALFIFI, 1977) and are presented with their adjusted coefficient of determination. Variables with a tolerance value < 0.2 were deleted from the model, to avoid multicollinearity problems. More conservative models were also computed, with the regression being halted after the last variable with a significant (p < 0.05) parameter entered the model.

RESULTS

COMPOSITION OF HERBIVORE FAUNAS

The estimation of regional species richness of insect folivores as recorded in the literature from Central Europe was highly correlated with the estimation of local species richness provided by the field survey (Table 1; r = 0.85, p < 0.001). Regional and local species richness also correlated with the total number of arthropod herbivores (insects and mites) recorded from corresponding British tree genera studied by KENNEDY and SOUTHWOOD (1984) (r = 0.98, p < 0.001 and r = 0.91, p < 0.01, respectively). The species richness of chewers, sap-suckers, leaf miners and gall formers was similarly well correlated between local and regional scales (r = 0.75, 0.88, 0.78 and 0.76, respectively, p < 0.001 in all cases). Although these general correlations appear to be good, Table 1 suggests that assessments of local herbivore richness may have been underestimated by the field survey on the following plants: *Salix, Quercus, Lathyrus, Euphorbia* and *Solidago*. In particular, few Chrysomelidae and Symphyta were collected from *Quercus* and *Salix*; no leaf miners from *Lathyrus*; few leaf miners and Chrysomelidae from *Euphorbia*; and no Lepidoptera from *Solidago*. It may also be of interest to note that, with

TABLE 2.

Independent variables determined for each host and used in multiple regression analyses. Variables indicated with '*' were determined empirically.

Coding variable	Description
Lwc *, Lwcy *	leaf water content of young and mature leaves [% DW]
Slw *, Slwy *	specific leaf weight of young and mature leaves leaves [g-4 x cm-2]
Chemic	number of broad categories of chemical defences (see text)
Disschem	dissimilarity of chemical defences with an average and hypothetical host (see text)
Congensp	taxonomic relatedness: no. of congeneric species in AESCHIMANN and BURDET (1989)
Confamsp	taxonomic isolation: no. of confamilial species in AESCHIMANN and BURDET (1989)
Locasp *	no. of congeneric species present within the study site (1)
Abund	abundance of woody hosts in Switzerland (Anon., 1988) [1000 m^3]
Locabund *	local abundance (total no. individual censused, see text)
Aggrega *	local aggregation (coefficient of variation for local abundance, see text)
Distger	distribution in West Germany (no. of 10 x 10 km squares in HAEUPLER et al., 1988)
Distsw	distribution in Switzerland (no. sampling sectors in WELTEN and RUBEN SUTTER, 1982)
Distsg	distribution in West Germany and Switzerland (Distger + Distsw) (2)
Locadist *	local distribution (no. plots in which the host was present, see text)
Height	maximum height in AESCHIMANN and BURDET (1989) [cm]
Leafar *	leaf area of a single leaf/leaflet [cm^2]
Shape	leaf shape: 1 = entire; 2 = dented; 3 = lobed; 4 = dented-lobed
Width *	ratio max. width to max. length of leaf/leaflet
Compac *	foliage compactness (leaf area within 50 cm of branch, see text) [cm^2]
Pheno *	no. of days during which young leaves (leaves pale green and of tender texture) were observed within the study site in 1990
Hairs *	no. of hairs per cm^2 of area (leaf underside)
Habitats	no. of habitats occupied by the host in AESCHIMANN and BURDET (1989)
Areatot *	total sum of leaf area sampled [m^2]

(1) Determined on the basis of field notes and on the distribution atlas of WELTEN and RUBEN SUTTER (1982)
(2) Swiss sampling sectors represented in average 100 km^2.

the exception of *Solidago*, these plants are represented by many congeneric species which are often mentioned by their generic names in published insect faunas. At both the regional and local scales, woody plants sustained significantly more herbivore species than herbaceous plants (t = 5.61, p < 0.001 and t = 7.96, p < 0.001, respectively). The proportion of incidental insects collected was lowest in *Arum*, *Crataegus*, *Euphorbia* and *Solidago* (between 0 and 0.7 % of the total number of individuals censused, Table 3) and highest in *Paris*, *Orthilia*, *Mercurialis* and *Melittis* (between 8.7 and 48.0 %). In total, 2.2 % of insects collected from study hosts were considered to be incidentals.

The distribution of species within the different guilds, as recorded during the field survey, is indicated for each host in Fig. 1. At the regional scale, corresponding data were tested by contigency table analysis for non-uniformity. This showed that the distribution of species was significantly non-uniform among woody hosts (G-test, G = 121.0, p < 0.001), as already noted by CORNELL and KAHN (1989) for British trees, and also among

TABLE 3.

Local dependent variables recorded from host plants: index of herbivore abundance, number and percentage of specialist species, number of incidental insects collected, total number of individuals censused and mean scores obtained in feeding experiments (young and mature leaves, all leaves combined and number of insect species tested).

Host	Index	(s.e.)	Speciali	(Ratiospe)	Incid	Censused	Scoyoung	Scomatu	Scotot	n
Salix	1.94	(0.56)	33	(71.7)	14	405	35.3	36.1	35.6	49
Corylus	0.99	(0.17)	14	(45.2)	19	343	19.6	25.6	22.8	47
Fagus	2.26	(0.42)	18	(47.4)	19	793	45.2	36.8	42.1	68
Quercus	3.44	(0.41)	30	(62.5)	24	1046	36.8	22.1	29.3	57
Crataegus	3.88	(0.66)	24	(68.6)	1	343	31.0	18.5	26.1	51
Sorbus	1.87	(0.25)	15	(48.4)	9	643	24.3	20.6	22.6	47
Acer	2.68	(0.42)	17	(54.8)	15	1445	37.1	28.0	33.3	70
Fraxinus	0.95	(0.14)	12	(48.0)	6	342	30.4	8.6	20.5	62
Lonicera	1.54	(0.35)	17	(85.0)	11	183	12.9	14.1	13.5	53
Viburnum	1.72	(0.45)	12	(66.7)	18	687	10.5	15.7	13.5	52
Arum	0.59	(0.17)	0	(0)	0	17	0.2	0	0.1	35
Paris	0.44	(0.10)	3	(100.0)	2	23	0.2	8.0	3.2	36
Dentaria	1.33	(0.32)	9	(69.2)	15	174	0.6	10.1	4.1	41
Lathyrus	0.91	(0.22)	2	(25.0)	2	30	23.9	12.2	18.3	40
Euphorbia	13.89	(2.81)	4	(75.0)	2	469	5.9	13.5	8.9	43
Mercurialis	0.29	(0.07)	4	(66.7)	4	23	15.1	6.2	11.7	47
Orthilia	0.47	(0.16)	1	(33.3)	1	9	1.5	6.9	4.3	31
Melittis	0.34	(0.07)	2	(25.0)	12	25	0.7	1.8	1.0	33
Galium	1.17	(0.39)	2	(40.0)	1	27	0.5	0.1	0.4	37
Solidago	7.34	(0.87)	6	(85.7)	6	855	0.1	15.7	6.9	32

herbaceous hosts (G = 49.2, p < 0.01). The same type of distribution was also tested for non-uniformity between an average woody host and an average herbaceous host (sum of all species per guild in each host category). This revealed a significant influence of host architecture on the distribution of species within guilds (G = 34.4, p < 0.001): the proportion of leaf mining species was high in herbaceous plants, while that of chewers was high on woody hosts. Similar analyses were difficult to perform with local data because the frequencies were too low in many cells. However, comparison of average woody and herbaceous hosts showed no significant effect of host architecture at the local scale (G = 5.8, p = 0.122).

At the regional scale, the distribution of species within ectophagous and endophagous types was non-uniform among woody and herbaceous hosts (G = 46.0, p < 0.001 and G = 19.8, p < 0.05, respectively), and non-uniform between the average woody and herbaceous hosts (G = 4.5, p < 0.05). The latter sustained a high proportion of endophages. At the local scale the trends were different: the distribution was uniform among woody plants (G = 8.2, p = 0.516), non-uniform among herbaceous plants (G = 33.3, p < 0.001), and uniform between host categories (G = 0.1, p = 0.722).

HERBIVORE ABUNDANCE, HOST UTILIZATION AND INSECT HOST-SPECIFICITY

Mean abundances of insect folivores, as determined during the whole interval of the field survey, are presented in Table 3. They did not differ significantly between woody and herbaceous hosts (t = 0.38, p = 0.708), but the most extreme values were recorded on

FIG. 1.

Distribution of the number of species per guild, as recorded for each host during the field survey. Regional data are indicated below each host.

the latter (highest values: *Euphorbia* and *Solidago*; lowest values: *Mercurialis* and *Melittis*). Seasonal abundance of herbivores was significantly non-uniform among woody plants and among herbaceous plants (unpubl. data; G = 1659.7 and G = 3090.2, respectively, p < 0.001). Seasonal distribution was also non-uniform between average woody and herbaceous hosts (G = 1172.7, p < 0.001): herbivore abundance was high in late April - early May on the former, decreased in mid-July and rose again by mid-October, whereas on the latter, it increased until the end of June, fell sharply by early July and increased again later, but not as markedly as previously.

The number of species collected on young foliage, mature foliage and on both foliage types is indicated in Fig. 2. This provided only a rough idea of host utilization (i.e., the use

of young and mature foliage), because sampling effort differed between foliage types (on average 4 out of 11 sampling occasions were concerned with young foliage), and collection of an herbivore on a particular type of foliage does not imply that it can use it successfully. Contingency tests showed that "host utilization" was uniform among woody and herbaceous hosts (G = 9.8, p = 0.365 and G = 5.8, p = 0.759, respectively), and also between average woody and herbaceous hosts (G = 0.03, p = 0.865). A different assessment of host utilization by insect chewers was given by the scores obtained during feeding experiments (Table 3). In some instances, young foliage was apparently more palatable than mature foliage (*Fagus, Quercus, Crataegus, Sorbus, Acer, Fraxinus, Lathyrus* and *Mercurialis*), in other cases the opposite applied (*Corylus, Lonicera, Viburnum, Paris, Dentaria, Euphorbia, Orthilia* and *Solidago*), and there was no clear trend in others (*Salix, Arum, Galium* and *Melittis*). Paired t-tests indicated that palatability was not significantly different between young and mature foliage within woody (t = 1.97, p = 0.08) and herbaceous hosts (t = 0.97, p = 0.356). However, the palatability of both foliage types was much higher in woody than in herbaceous hosts (t = 5.79, p < 0.001).
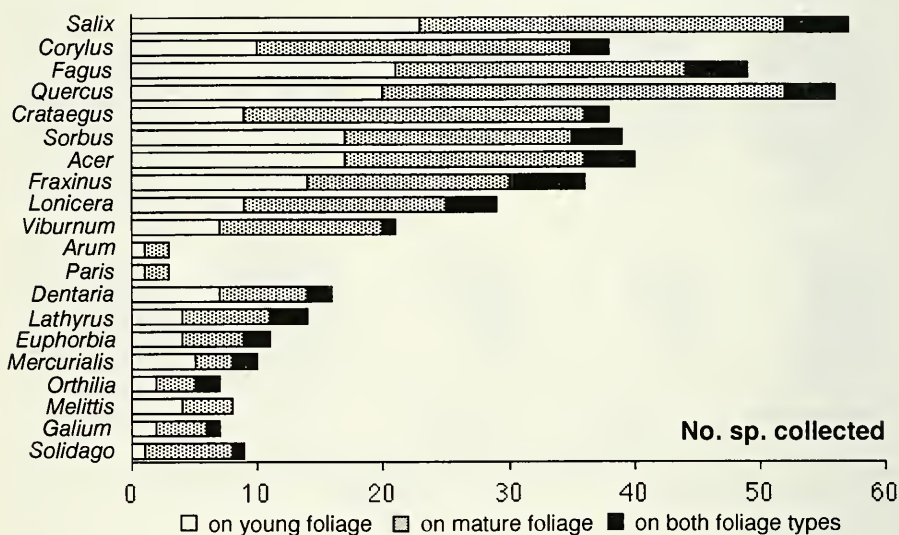
FIG. 2.

Number of species collected on different types of foliage during the field survey.

The number of specialist species (and their percentage of the total number of species) collected on each plant is indicated in Table 3. The highest specialist ratios were found on *Paris, Solidago, Lonicera, Euphorbia*, while the lowest occurred on *Arum, Lathyrus* and *Melittis*. Overall, these ratios were not significantly different between woody and herbaceous hosts (t = 0.72, p = 0.486), and, on average, amounted to 55.9 ± 5.38 % (s.e.) when all hosts were considered. Similarily, contigency table analysis did not reveal any influence of plant architecture on the distribution of species within specialist and generalist types (G = 0.6, p = 0.439). The scores for chewer species tested in feeding experiments are summarized in Fig. 3. Few species accepted more than 5 hosts as suitable for feeding. Both this data set and the former indicate that most of the insects collected were specialists.

FIG. 3.

Scores of feeding experiments for chewing species. The first class of score (100*) refers to the number of species which could only be tested once, on the host from which they were collected.

MULTIPLE REGRESSION ANALYSES

A correlation matrix for selected dependent variables is presented in Table 4. A weak positive correlation existed between the overall abundance of herbivores and the palatability of mature leaves. This suggested that this last factor was important for large build-ups of herbivore populations during the growing season. The proportion of special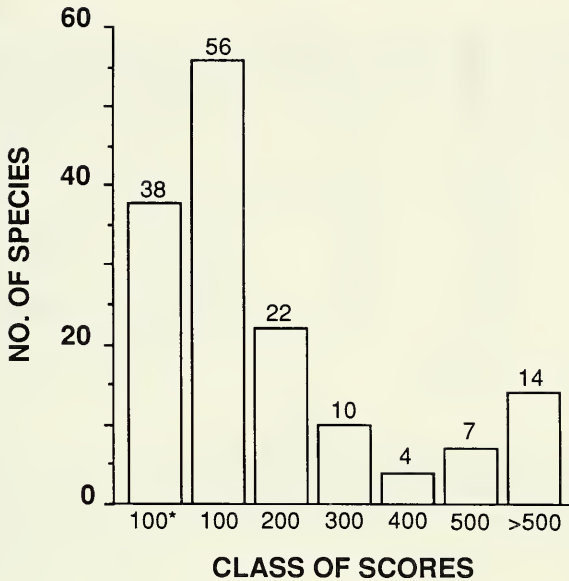ists was not correlated significantly with herbivore abundance. The species richness and the proportions of specialists and ectophages were positively correlated with the palatability of leaves, particularly that of young leaves.

The results of multiple regressions analyses are detailed in Table 5, with particular reference to the composition of herbivore communities at the regional and local scales. For the former, 85 % of the variance was explained by the height of the host, its taxonomic relatedness, water content of young leaves, and, to a lesser extent, by its taxonomic isolation. At the local scale, 88 % of the variance could be explained, with height and host phenology entering first and second in the regression. In general, the predictors of models for regional and local data were different. The local species richness of chewers could only be significantly accounted for by the total leaf area sampled, a measure of the sampling effort, and water content of young leaves.

Table 6 summarizes the multiple regressions with particular reference to plant architecture. The predictors were also quite different between host categories. For woody hosts, 58 % of the variance could be accounted for by the number of habitats in which the host grows and its height (regional data). In contrast, 69 % of the variance was explained in herbaceous plants by leaf width. The number of insect specialists collected on these hosts depended also upon leaf width.

TABLE 4.

Lower correlation matrix (Pearson coefficient) for selected dependent variables.

	Index	Ratiospe	Scoyoung	Scomatu	Ratioect
Ratiospe	0.35	–	–	–	–
Scoyoung	0.18	0.29	–	–	–
Scomatu	0.45 *	0.63 **	0.70 ***	–	–
Ratioect	–0.06	0.29	0.66 **	0.54 *	–
Ratioend	0.26	–0.15	–0.16	–0.25	–0.78 ***
Nospecie	0.25	0.35	0.82 ***	0.72 ***	0.57 **
Nospecto	0.49 *	0.40	0.77 ***	0.75 ***	0.42

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

TABLE 5.

Summary statistics of stepwise multiple regression analyses performed on the 20 hosts, with particular reference to the composition of herbivore communities at the regional and local scales. The order of the variables in the final equation follows the step in which they entered the regression. Data in brackets indicates the R^2 of the conservative model (see text), and the corresponding number of variables which entered the regression (same order, starting from the left).

Dep. var.	Regression equation	R^2	F-test	(R^2, n)
(a) Regional data				
Nospecto	11.79 + 0.60 Height*** + 0.49 Congensp**			
	- 2.95 Lwcy* + 0.20 Confamsp	0.85	28.9***	(0.83, 3)
Chwto	6.60 + 0.48 Height*** + 1.96 Pheno***			
	- 3.78 Width** - 3.22 Lwc	0.83	24.1***	(0.80, 3)
Sapto	14.09** + 0.53 Height*** - 3.40 Lwcy**			
	+ 0.25 Congensp*	0.90	56.3***	–
Mineto	13.05 - 3.56 Lwc* + 0.92 Habitats			
	+ 0.37 Congensp* + 0.34 Confamsp*			
	+ 0.29 Height*	0.76	13.1***	(0.60, 2)
Gallto	-0.10 + 0.28 Height** + 0.37 Congensp*			
	-3.23 Disschem	0.60	10.4***	(0.53, 2)
(b) Local data				
Nospecie	-2.98** + 0.40 Height*** + 0.78 Pheno**	0.88	72.2***	–
Chw	11.06 + 0.50 Areatot** - 3.53 Lwcy**	0.72	25.6***	–
Sap	-5.05*** + 0.31 Height*** + 0.88 Pheno***			
	+ 0.72 Chemic**	0.93	80.5***	–
Mines	13.94*** - 3.34 Lwc*** + 1.11 Habitats**	0.69	22.6***	–
Galls	0.03 + 0.18 Height** - 2.04 Disschem*	0.64	17.6***	

Significance of parameter estimates: *$p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 7 details the models relevant to local independent variables. Herbivore abundance was related principally to the number of habitats in which the host grows, its distribution in Switzerland and its local aggregation. The number of specialist species was dependent upon the height and the phenology of the host. The proportions of specialists, ectophages and endophages could not be adequately explained by our variables. The palatability of the different types of foliage depended on several predictors, among which were more particularly sampling effort and leaf water. Not surprisingly, sampling effort was the most significant predictor explaining the number of incidental insects collected, but there were also weak contributions from host aggregation, chemical defences and pubescence.

TABLE 6.

Summary statistics of stepwise multiple regression analyses performed with particular reference to host architecture. Presentation follows Table 5.

Dep. var.	Regression equation	R^2	F-test	(R^2, n)
(a) Woody plants				
Nospecto	-0.84 + 2.22 Habitats* + 0.50 Height*	0.58	7.3*	–
Nospecie	15.21** - 2.87 Lwc**	0.56	12.4**	–
Speciali	Not significant	–	–	–
(b) Herbaceous plants				
Nospecto	4.74*** - 5.76 Width**	0.69	20.8**	–
Nospecie	0.23 + 0.20 Confamsp* -0.22 Distsg*			
	+ 0.54 Pheno	0.75	9.8**	(0.67, 2)
Speciali	2.54*** - 3.57 Width*	0.53	11.0*	–

TABLE 7.

Summary statistics of stepwise multiple regression analyses performed for local dependent variables. Presentation follows Table 5.

Dep. var.	Regression equation	R^2	F-test	(R^2, n)
Index	5.57** + 1.68 Habitats*** - 0.62 Distsw**			
	- 0.42 Aggrega* - 0.18 Leafar	0.56	7.0**	(0.51, 3)
Speciali	-5.43** + 0.38 Height*** + 1.22 Pheno**	0.79	36.1***	–
Ratiospe	Not significant	–	–	–
Ratioect	34.17** - 7.24 Lwcy*	0.25	7.5*	–
Ratioend	Not significant	–	–	–
Scoyoung	13.46 + 0.50 Height*** - 3.98 Lwcy*			
	+ 1.73 Chemic	0.70	15.7***	(0.66, 2)
Scomatu	17.50* + 0.35 Areatot* -3.73 Lwcy*			
	- 1.62 Chemic*	0.66	13.5***	–
Scotot	9.35 - 3.46 Lwc** + 0.38 Areatot* + 0.74 Pheno	0.74	18.9***	(0.71, 2)
Incid	1.40 + 0.48 Areatot*** - 0.44 Aggrega			
	- 1.49 Chemic* + 0.11 Hairs	0.76	15.7***	(0.66, 1)

DISCUSSION

SAMPLING PROCEDURE

The limitations of our study are straightforward. Local estimates of species richness rely on data obtained during only a 7-month field survey. The number of sibling species may have been underestimated in the field, but there is no reason to believe that this factor was biased towards particular host plants. Sampling bias appeared identical among hosts, but insects associated with trees were collected from low branches only (sampling effort as measured by the total leaf area sampled is a different problem which is addressed below). The insect data are valid for common species, easy to discover on the foliage during day-time. Some herbivores may spend most of their time hidden in the leaf litter, and may feed on their hosts during short periods only. Those species, along with nocturnal and highly active ones, are likely to have been underestimated by the field survey. Increasing the

number of sampling occasions might also have increased the contrast in species richness between particular hosts. Furthermore, our data set is relevant only to part of a particular plant community, namely plants growing in woodlands of the collinean level. Inclusion of other plant species, particularly those growing in different habitats, might have altered the patterns described.

REGIONAL AND LOCAL PATTERNS OF SPECIES RICHNESS

The general correlation between estimates of species richness at the regional and local scales was good. In particular, estimates of local species richness were close to those of regional richness for plants which, presumably, are infrequently surveyed by entomologists and/or cited in insect faunas (e.g., *Melittis*, *Mercurialis*, *Arum*). However, the predictive models for herbivore species richness at the regional and local scales differed greatly in terms of the relative contribution of the significant variables. Some ecological factors - such as local aggregation and phenology of the host - may act as significant selective agents, influencing locally the commonness and rarity of certain species. However, their influence may be cancelled out at the regional scale, i.e., when host attributes are examined over a larger number of ecological situations and habitats. CORNELL (1985) pointed out that if local interactions are strong, then correlation between species richness at the regional and local scales should be weak. However, the regional data of our study do not formally represent regional data sensu CORNELL (1985), since both distributional and insect data did not relate to the entire geographical range of host plants, because of the lack of suitable data (see below).

INFLUENCE OF PLANT ARCHITECTURE ON OBSERVED PATTERNS

The slight increase in herbivore density observed on most woody hosts in mid-October corresponded probably to searching for hibernation sites and, thus, appeared to be directly related to plant architecture. Herbaceous plants sustained a higher proportion of leaf mining species, and, more generally, of endophages, than did woody hosts. However, these trends were more marked for regional data than for local data. Concealment of species in herbaceous plants is likely to be related to several factors. Amongst others, avoidance of predators and parasitoids and/or weather effects may be crucial when the architecture of the host is relatively simple. At the local scale, herbivore abundance and proportion of specialists were not significantly different between the two host categories. Although the last observation was unexpected, the variance in the proportion of specialists was much higher in the case of herbaceous than woody hosts. This suggests that biochemical conditions for herbivores are more varied in the former than in the latter. Indeed, out of the 14 species which could be considered as highly generalist (feeding score > 500), only one was collected from herbaceous plants. Different authors have emphasized that non-apparent plants, such as herbs, may have evolved towards chemical diversification (e.g., FUTUYMA, 1976; SCRIBER and FEENY, 1979). At both regional and local scales, herbivore species richness was differently explained on woody and herbaceous hosts but there was no obvious contribution of plant biochemistry (hovewer, see discussion of this variable below).

HOST-RELATED VARIABLES AND THEIR PREDICTIVE VALUES

The effects of certain variables, which were determined locally, such as water content of young and mature leaves and host phenology, were significant at the regional scale.

However, it remains to be seen if their predictive value is really significant when intraspecific differences are accounted for, when average values are determined over most of the area of distribution of hosts, and when host plants growing in different habitats are included in the analyses.

Sampling effort, as represented by the total leaf area sampled per host, had a significant effect in the models describing the local species richness of chewers, the number of incidental insects collected and the palatability of mature leaves. That effect was primarily due to sampling of much smaller foliage areas for herbaceous hosts than for woody hosts (Appendix 1), a deliberate procedure to maximise time investment during sampling. After removing the effect of sampling, in testing residuals as dependent variable, leaf water and leaf area only had a significant effect on the local species richness of chewers, but the variance explained was low ($R^2 = 0.30$). These conclusions differ slightly from those of KARBAN and RICKLEFS (1984) who found that, after removing the effect of sampling effort, Lepidoptera species richness could not be explained significantly by chemical traits (including leaf water) of the foliage of 33 deciduous tree species in Ontario.

The height and the leaf water of the host were important predictors in the various models tested. They may reflect differences in plant architecture, but also seem to possess intrinsic predictive power. This was demonstrated by introducing a dummy variable accounting for plant architecture: this variable did not enter in the regressions describing species richness at the regional scale, and when it entered in other models, it did not totally cancel the effect of height and leaf water. No satisfactory estimation of total leaf area for woody hosts, which would probably have been highly correlated with height, could be introduced in the models. Total leaf area did not significantly affect herbivore species richness on herbaceous plants. Since leaf water is usually correlated with leaf nitrogen and limits its assimilation, this factor is important in the nutrition of insect herbivores (MATTSON and SCRIBER, 1987). However, leaf water was negatively correlated with species richness. This may be related to the observation that leaf water content often reflects different strategies of plant chemical defences, such as the distribution of carbon- and nitrogen-based secondary compounds (MATTSON and SCRIBER, 1987). Alternatively, plants with low water content may grow in sunny or xeric conditions, which, in turn, may be more suitable for sylvestral herbivores exploiting cool and shady habitats, such as reported here. Since leaf water is likely to vary through seasonal and daily cycles (SCRIBER, 1977), the analyses presented here, which are based on discrete leaf water measurements, should be confirmed by more extensive studies.

NIEMELÄ and HAUKIOJA (1982) presented evidence that the extent of the shoot-growth period in deciduous trees affects the seasonal distribution of Macrolepidoptera species richness. Furthermore, RAUPP et al. (1988) showed that the distribution of some generalist Lepidoptera is strongly influenced by phenological differences in host suitability. In our study, an estimation of the number of days during which young leaves were available at the study site proved useful for predicting the regional species richness of chewers, the local species richness of folivores in general, of sap-suckers and of specialists. Young leaves were still available on certain tree species after most of the foliage had matured (particularly on *Salix*), or secondary shoot-growth occurred during summer. These "islands" of young foliage often sustained high grazing damage, as reported in NIEMELÄ and HAUKIOJA (1982), and might have increased herbivore species richness locally. These observations remain to be tested at the regional scale. They are unlikely to be general and will probably depend on the particular host plants included in the analyses, since the palatability of young leaves was not always higher than that of mature leaves.

Taxonomic relatedness and isolation, as represented by the variables Congensp and Confamsp, contributed significantly to several models at the regional scale. These observations concur with other studies (see introduction). Since Congensp and Congenfam accounted for additional and different proportions of the variance in the models, with the former variable being often more significant, this suggests that their effects may be more important respectively for monophagous and oligophagous insects. The "local" taxonomic isolation of the host appeared less important and, in contrast with other studies (e.g., KENNEDY and SOUTHWOOD, 1984), the number of plant species recorded within the plant order of the host explained less variance than the previous variables.

Many authors studying models of herbivore species richness on their hosts considered that at least some of the variance left unexplained could be attributed to the chemical defences of the host (e.g., CLARIDGE and WILSON, 1982; JONES and LAWTON, 1991). In our study, this factor influenced marginally some of the models tested, but this need not imply that it has little influence on herbivore species richness. Other variables, such as taxonomic relatedness and isolation (CLARIDGE and WILSON, 1982) may better describe the influence of host biochemistry. The number of broad chemical categories accounted for a small proportion of the variance in local species richness of sap-suckers and in the palatability of the foliage. However, it was a very crude index of the diversity of chemical defences, since it did not contain information about the concentration levels and the chemical diversification of secondary compounds within the categories of defences defined. The chemical dissimilarity with an hypothetical host accounted for some variance in the regional species richness and the local number of gall forming species. This variable is as good as the choice of the average host. In this simple analysis, the average host turned to be equivalent to *Quercus* (Appendix 1), and, therefore, it was not surprising that the variable Disschem influenced the model describing the number of gall forming species, which are well-diversified on *Quercus* (e.g., BUHR, 1964-1965).

The regional distribution of host did not contribute to the variance in herbivore species richness at the regional scale. Although species-area relationships account for a significant proportion of the variance (20-90 %) in species richness (references cited in the introduction), recent analyses by CLARIDGE and EVANS (1990) showed that using more accurate distributional data may result in a sharp decrease of the variance explained. Currently, distribution maps of all study hosts are not available for Europe, or for Central Europe. We chose the Swiss and German data as a substitute for regional distribution because they were accurate and concerned adjacent areas. Data covering more extended and adjacent regions of Europe would have probably increased the importance of host regional distribution for herbivore species richness. Another related variable, local host aggregation, was important in some models, whereas local host distribution and abundance were insignificant.

Although most of the hosts analysed included plants growing in woodlands only, the number of habitats occupied by the host was also important in several of our models, as reported in other studies. Inclusion in the analysis of other plants growing in various habitats would have probably increased further the significance of this factor. Lastly, the age of establishment of the host could not be considered in our analyses, since similar data as are available for trees (BIRKS, 1980) were not available for shrubs and herbaceous plants.

PREDICTIVE MODELS FOR INSECT TROPHIC CATEGORIES AND HOST-SPECIFICITY

To date, the information compiled for British trees by KENNEDY and SOUTHWOOD (1984) represents the best regional-scale data of this kind. CORNELL and KAHN (1989) used

this data set to predict insect species richness by trophic categories. They found that between 54 % and 83 % of the variance, depending on insect guild, could be explained by host abundance, taxonomic isolation, age of establishment and "evergreenness". The present study suggests that an additional part of the variance could be accounted for by leaf water-content and host phenology. Inserting leaf water in the model describing species richness of British data (7 tree genera were common to both studies) resulted in an improvement from 38 % of variance explained (only tree abundance significant) to 62 % (tree abundance first, leaf water second).

ZWÖLFER and BRANDL (1989) suggested that the organization of endophytic herbivore communities is more structured than that of ectophytic herbivore communities. Assuming that a highly structured community should also be highly predictable, our data neither support nor refute their hypothesis, as proportions of endophagous and ectophagous species were both difficult to predict. Most information available regarding the proportion of specialist species feeding on particular host plants has been obtained from compilation of insect faunas. For instance values reported by NEUVONEN and NIEMELA (1981), ROWELL-RAHIER (1984) and LEATHER (1985) range from 10 % to 66 %. The high proportions of specialists reported in the present study (average 56 %) result probably from the bias of the sampling procedure towards abundant species, which are more likely to be specialists (see GASTON and LAWTON, 1988). Although the effect of sampling effort was controlled in our study, no model could be satisfactorily fitted to account for the proportion of specialists. This contrasts with the variance explained in herbivore and specialist species richness (88 % and 79 %, respectively) and emphasizes how much is still to be learnt in the field of insect-plant interactions. Despite the significant effects of sampling effort, the number of incidental insects collected appeared to be related to host aggregation and chemical defences. These factors may be important in processes of host colonization by introduced insect species.

In conclusion, this study revealed that some host-related attributes, rarely considered in other studies of a similar kind, may have some predicting power in models describing the organisation of herbivore communities on their host plants. Other host-related attributes which were not considered here, such as the history of interactions between insects and their hosts, and the genetic variability of the host population (MADDOX and ROOT, 1990), may also have significant effects on herbivore communities. Furthermore, this is likely to be true of other variables not directly related to the host, such as the local abundance and foraging efficiency of predators/parasitoids, and the history of speciation within insect taxa. Integration of all of these factors, if possible, should greatly improve our understanding of insect-plant interactions.

APPENDIX 1.

Selected independent variables used in multiple regression analyses. Coding variables and units as in Table 2.

Host	Lwc	Lwcy	Height	Chemic	Disschem	Locabund	Aggrega	Distger	Distsw	Locadist	Congensp	Confamsp	Width	Pheno	Habitats	Areatot
Salix	59.4	66.6	1000	5	0.365	7	424.3	2016	341	3	28	32	0.50	162	4	14.7
Corylus	61.5	67.4	900	4	0.258	23	223.8	2017	320	12	1	10	0.76	102	2	18.7
Fagus	54.5	70.5	3500	4	0.258	425	65.2	2013	289	49		6	0.69	104	1	19.8
Quercus	51.5	65.2	4000	5	0	50	221.7	1541	225	13	4	6	0.60	128	2	16.4
Crataegus	54.4	53.7	400	6	0.447	13	239.9	1885	254	9	2	137	0.65	128	2	4.6
Sorbus	54.6	67.5	1500	5	0.365	97	126.6	600	331	32	6	137	0.67	104	2	27.8
Acer	58.3	67	1200	4	0.258	147	156.5	1	48	34	6	6	1.23	130	1	40.0
Fraxinus	65.4	75.9	3500	6	0.447	59	186.2	2039	302	23	2	6	0.40	55	1	17.0
Lonicera	65.2	73.7	200	5	0.365	98	132.3	1313	323	31	8	15	0.61	122	2	3.3
Viburnum	64.3	60.3	250	6	0.258	33	184.5	743	283	14	2	15	0.70	131	2	25.7
Arum	88.9	86.8	50	6	0.447	10	693.0	1165	210	1	2	4	0.80	71	2	1.3
Paris	78.1	81.9	30	5	0.632	58	338.8	1488	302	7	1	67	0.60	62	1	2.3
Dentaria	80.0	79.9	60	3	0.516	243	250.5	10	101	16	5	149	0.27	89	1	9.1
Lathyrus	68.8	76.7	35	6	0.447	175	214.4	722	226	22	18	150	0.35	84	1	3.2
Euphorbia	71.5	66.3	60	6	0.447	184	159.3	244	122	22	20	23	0.29	96	2	2.1
Mercurialis	74.6	79.1	35	8	0.447	1421	130.9	1514	272	34	3	23	0.44	99	1	4.8
Orthilia	61.9	74.2	20	4	0.258	52	385.5	447	254	4	1	8	0.69	60	1	0.9
Melititis	70.0	78.6	50	6	0.447	217	123.9	154	117	37	1	78	0.44	49	1	3.9
Galium	69.7	83.3	30	6	0.258	794	138.9	1557	282	27	32	30	0.24	92	1	0.6
Solidago	72.0	83.5	90	4	0.447	248	168.9	1746	380	32	4	309	0.20	82	5	5.0

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